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Partial drying accelerates bacterial growth recovery to rewetting

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ABSTRACT

Fluctuations in soil moisture create drying-rewetting events affecting the activity of microorganisms. Microbial responses to drying-rewetting are mostly studied in soils that are air-dried before rewetting. Upon rewetting, two patterns of bacterial growth have been observed. In the Type 1 pattern, bacterial growth rates increase immediately in a linear fashion. In the Type 2 pattern, bacterial growth rates increase exponentially after a lag period. However, soils are often only partially dried. Partial drying (higher remaining moisture content before rewetting) may be considered a less harsh treatment compared with air-drying. We hypothesized that a soil with a Type 2 response upon rewetting air-dried soil would transform into a Type 1 response if dried partially before rewetting. Two soils were dried to a gradient of different moisture content. Respiration and bacterial growth rates were then measured before and during 48 h after rewetting to 50% of water holding capacity (WHC). Initial moisture content determined growth and respiration in a sigmoidal fashion, with lowest activity in air-dried soil and maximum above ca. 30% WHC. Partial drying resulted in shorter lag periods, shorter recovery times and lower maximum bacterial growth rates after rewetting. The respiration after rewetting was lower when soil was partially dried and higher when soils were air-dried. The threshold moisture content where transition from a Type 2 to a Type 1 response occurred was about 14% WHC, while >30% WHC resulted in no rewetting effect. We combine our result with other recent reports to propose a framework of response patterns after drying-rewetting, where the harshness of drying determines the response pattern of bacteria upon rewetting dried soils.

1. Introduction

Moisture is an important determinant of microbial activity in soil (Manzoni et al., 2012a). Fluctuations in moisture conditions create drying and rewetting events, which affect microbial growth rates and soil respiration rates (Kieft et al., 1987; Blazewicz et al., 2014), and it is well known that a pulse of carbon dioxide (CO_2) often is observed after rewetting a dry soil (Jarvis et al., 2007; Sponseller, 2007; Kim et al., 2012). Most studies of drying-rewetting events assess completely air-dried soils that are rewetted to optimal moisture (Chowdhury et al., 2011; Barnard et al., 2015; Meisner et al., 2015), but soil moisture content will vary spatially (Rey et al., 2017) and temporally (Cregger et al., 2012). Thus, the moisture content before rewetting will vary and is frequently much higher than in air-dried soils (Lado-Monserrat et al., 2014). The increase in respiration rate induced by rewetting has been shown to be less evident when soil is partially dried before rewetting (Kim et al., 2010; Yan and Marschner, 2014) and is only detectable when soil is dried to a moisture content below a threshold level (Fischer, 2009). Thus, rewetting completely air-dried soils could be considered a harsher perturbation than rewetting partially dried soils. It is generally assumed that the size of the respiration pulse will correlate with the amount of microorganisms killed by the drying-rewetting event (Kieft et al., 1987; Blazewicz et al., 2014; Fraser et al., 2016), although mobilization of carbon (C) released from soil organic matter (Xiang et al., 2008; Schimel et al., 2011) or the accumulation of osmolytes in microbial biomass (Warren, 2014; but see Boot et al., 2013) will also contribute to the respiration pulse.

Two patterns of bacterial growth have been observed upon rewetting a dry soil (Fig. 1). In the first pattern ("Type 1 response"; Fig. 1), bacterial growth rates increase linearly from low values

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upon rewetting without a lag period (Iovieno and Bååth, 2008). In the second pattern ("Type 2 response"; Fig. 1), bacterial growth rates start to increase exponentially after a clear lag period of up to 20 h of very low levels of bacterial growth (Göransson et al., 2013). These differences in growth patterns also result in a shorter recovery time for the Type 1 response, and higher rates of maximal growth in the Type 2 response (Meisner et al., 2015). Previous work showed that a prolonged drying period can shift the response pattern from a Type 1 to a Type 2 within the same soil (Meisner et al., 2013, 2015). It was hypothesized that a lower survival of microbes due to prolonged drying was the reason for this shift in response pattern (Meisner et al., 2015), suggesting that a harsher treatment would result in a Type 2 response with increasingly longer lag periods.

Since partial drying could be considered a less harsh treatment than air-drying, we hypothesized that a soil with a Type 2 response to rewetting air-dried soil would transform into a Type 1 response if dried only partially before rewetting (Fig. 1). As such, the aims of the current study were: (1) to test how partial drying affect the bacterial growth response upon rewetting a soil with a Type 2 response; (2) to determine at what moisture level the transition from a Type 2 into a Type 1 occurs. We expected that partial drying before rewetting would result in shorter lag periods before the increase of bacterial growth, lower maximum growth rates after rewetting and a shorter recovery time to values matching those in a constantly moist soil compared to air drying. In addition, we expected that partial drying before rewetting would result in a lower CO_2 release upon rewetting. A prerequisite for our study was that respiration and bacterial growth rates are reduced at lower water contents before rewetting (Iovieno and Bååth, 2008; Manzoni et al., 2012a).

2. Material and methods

2.1. Soil

Selected soils exhibited a Type 2 response after rewetting following 4 days' air drying, with an increase in bacterial growth after lag periods of around 15–20 h at 17 °C. Soil from Greenland was collected in August 2014 at Østerlien, which is located close to the Arctic Station, Qeqertarsuaq, Disko Island in Central West Greenland. The soil at this site was formed by quaternary deposits

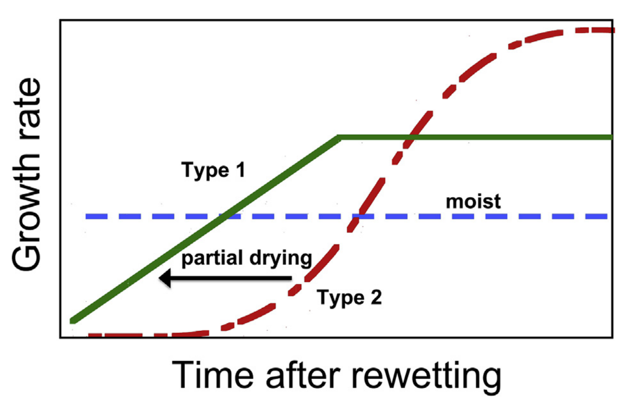

Fig. 1. Schematic overview of the two response patterns of bacterial growth found after drying-rewetting. In a Type 2 response (red stippled line), bacteria increase their growth rates after a clear lag period, whereas in a Type 1 response (green line), bacteria increase their growth rate linearly immediately after rewetting. The blue line indicates the bacterial growth rate in the constantly moist control soil. The arrow indicates the hypothesis that partial drying before rewetting changes the Type 2 into a Type 1 response. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on pre-quaternary formations of crystalline, breccia and plateau-basalt lavas, of the order Gelisols (USDA, 1992) or Cryosols (FAO, 1989). The soil was sampled from the A-horizon (pH_{water} = 6.7; SOM = 5.7%). Soil from the U.K. was collected in August 2014 at the Henfaes Experimental Research Station, which is located 12 km east of Bangor, U.K. The soil was a fine loamy brown earth over gravel (pH_{water} = 5.3; SOM = 8.4%) classified as a Dystric Cambisol (FAO, 1989) or a Fluventic Dystrochrept (USDA, 1992) and was collected under ca. 12 year old Alder (*Alnus glutinosa*) or Beech (*Fagus sylvatica*) monocultures describes previously (Göransson et al., 2013). All soils were sieved (<2.8 mm) fresh, and stones and roots were picked out by hand. Soils were stored at 4 °C until use.

2.2. Experiments

Four experiments were made. For the U.K. soils, the alder and beech forest soils were treated as replicate experiments. The Greenland soil was only sampled at one place, but two separate experiments with this soil were made in order to replicate the experiment. We combined non-independent experimental assessments of the same location for curve fitting.

2.2.1. Drying of soils

The soils were dried at room temperature (22–23 °C) under a fan until they reached the intended range of water contents. Before drying, 50 g field moist soil was placed into 500 ml microcosms and adjusted to 50% of its maximum water holding capacity (WHC). The time to reach the desired water content varied from 0 h (for 50% WHC) to 2 days (for air-dried soils). Once the approximate moisture content was reached, the microcosms were lidded and the water content was determined gravimetrically.

All the microcosms were placed at 17 °C and kept with lids closed for 1–4 days. Then bacterial growth and respiration were measured in the moisture gradient of soils one day before rewetting to estimate the direct effect of moisture content on growth and activity. The growth rate assessments used 1 h incubations and the respiration rate assessments used 24 h.

2.2.2. Rewetting of soils

Dried soils were rewetted to 50% WHC and incubated at 17 °C together with a moist control always kept at 50% WHC. Upon rewetting, bacterial growth was measured every 2–3 h during 48 h. To allow this sampling scheme, two sets of soils were prepared from each microcosm on the day of rewetting by placing 15 g subsamples of soil into 150 ml plastic vials. One set was rewetted in the evening and one set the following morning to allow for response curves with a high temporal resolution as has been performed previously (Meisner et al., 2013, 2015).

2.3. Microbial analyses

2.3.1. Bacterial growth

Bacterial growth was measured by the incorporation of ^{3}H-Leucine (Leu) into extracted bacteria (Bååth et al., 2001). Briefly, at each time point, one gram of soil was mixed with 20 ml demineralized water by vortexing for 3 min. The supernatant with a bacterial suspension was sampled after low speed centrifugation (1000 *g* for 8 min) and the incorporation of Leu was measured in 1.5 ml aliquots of the bacterial suspension. A combination of non-radioactive and tritiated Leu ([^{3}H]Leu, 37 MBq ml^{-1}, 5.74 TBq $mmol^{-1}$, Perkin Elmer, USA) was added to yield a final concentration of 275 nM. The extracted bacteria were incubated for 1 h at 17 °C. The samples were washed (Bååth et al., 2001) and the radioactivity of the incorporated Leu was measured on a liquid scintillator. Bacterial growth was expressed as the amount of Leu that was incorporated in the extracted bacteria per g dry soil and per h.

2.3.2. Soil respiration

Soil respiration was measured using a GC equipped with a methanizer and a FID detector. One gram of soil was put in a 20 ml glass vial, purged with pressurized air, sealed and incubated at 17 °C for 24 h. Three time periods were measured: 24 h before rewetting, 0–24 h after rewetting and 24–48 h after rewetting. The respiration rates were expressed as µg CO_2 per g dry soil and per day.

2.4. Modeling

2.4.1. Modeling bacterial growth

Bacterial growth and respiration values were standardized for the response by the maximum value for bacterial growth and respiration before rewetting. After rewetting, the standardization was done by dividing with the activity in the 50% WHC moist control soil. This standardization was done to be able to compare bacterial growth and respiration rates against soil moisture for the four experiments.

Since two response patterns of bacterial growth are found after rewetting, two types of models were used to calculate the lag period (time before bacteria start growing exponentially), maximum growth rate and recovery time (the time point where bacterial growth reached the value in the constantly moist control soil (50% WHC)) (Meisner et al., 2015). Curves were fitted using Kaleidagraph version 4.5.2 for Mac.

When bacterial growth started to increase exponentially after a lag period (Type 2), the response was modeled with the modified Gompertz equation (Zwietering et al., 1990) for the period before the maximum growth rate of the bacteria was reached:

$$G_t = B + \left\{ A^* e^{\left(-e^{\left(\frac{\mu_{max}{}^* e}{A} (\lambda - t) + 1 \right)} \right)} \right\} \tag{1}$$

G_t is the standardized growth rate at time t. B is the asymptotic growth rate at t_0, that is initial growth rate before rewetting. A is the difference between the lower and higher curve asymptotes. μmax is the specific bacterial growth rate. λ is the lag time, the time point after which growth starts to increase exponentially. The recovery time point is the time point where G_t equals growth in the moist control, and maximum growth rate was calculated as the sum of A and B.

When bacterial growth started to increase immediately upon rewetting (Type 1) the response was modeled with a linear function until the growth rate was stable. The linear model was also used when it was not possible to fit a Gompertz equation or the model fit for the Gompertz equation was below $R^2 = 0.75$. The lag period for the linear model was per definition 0 h for this response type. The recovery time point was the time point where growth calculated with the linear function equaled growth in the moist control, and maximum growth was calculated as the average growth rate for all the measurements after stable growth was reached.

2.4.2. Modeling the relationships between moisture and characteristics of activity

The relationships between soil moisture and bacterial growth as well as soil moisture and soil respiration were modeled with a logistic equation. The relationships between soil moisture before rewetting and lag time or recovery time were also modeled with a logistic equation. The relationships between soil moisture content before rewetting and maximum growth rates or respiration rates after rewetting were modeled with a negative exponential equation. We checked if the data from the two sites could be combined into one curve fit by calculating the F-ratio that was based on the sum of squares and degree of freedoms of both fits separate and the sum of squares when the model was fit with all data (Motulsky and Ransnas, 1987). A large F value indicated that two separate curve fits for each site was better (Table S1).

Before rewetting, we considered a lower threshold moisture level when there was no further decrease in growth or respiration with decreasing % WHC and a higher threshold value (saturation) when there was no further increase in response variables with increasing % WHC. After rewetting, we considered the presence of a threshold when there was no further increase with decreasing % WHC and a saturation point when there was no further decrease with increasing % WHC. The threshold and saturation values for the logistic equations were calculated according to McDowall and Dampney (2006). In brief, the y-value at 0.05 and 0.95 of the curve is calculated and we considered the corresponding x-values as the threshold and saturation value, respectively. For the negative exponential equations, we considered the x-value when modeled y-values exceeded 0.05 of the difference between maximum and minimum values of the curve.

3. Results

3.1. Respiration and bacterial growth before rewetting

Both bacterial growth and respiration rates increased with soil moisture content according to a logistic model (Fig. 2). The respiration and growth rates did not increase further above around 30% WHC, with half of maximum rates around 15% WHC. A lower threshold was found around 3% WHC, which was similar to moisture content in air-dried soil. The similar effect of moisture content before rewetting on bacterial growth and respiration rate made them positively correlated at an almost 1:1 relationship (Fig. 3; $R^2 = 0.90$; $P < 0.001$).

3.2. Bacterial growth after rewetting

Moisture content before rewetting affected the bacterial growth pattern after rewetting (Fig. 4). A Type 2 response with a clear lag period followed by an exponential increase in growth rate was observed when soils were air-dried or dried to low soil moisture contents before rewetting in both soils. For example, rewetting air-dried soil (~3% WHC) from Greenland resulted in a lag period of around 20 h (Fig. 4a). The lag period then became shorter when soil was dried less severely prior to rewetting in both the Greenland (Fig. 4a) and the U.K. soils (Fig. 4b). An exponential growth increase was still found after the lag period when there was a Type 2 response. At even higher remaining initial moisture content before rewetting, bacterial growth started at higher levels and also started to increase immediately in a linear fashion, showing a Type 1 response.

The relationship between soil moisture content before rewetting and the length of the lag period was modeled with a logistic relationship ($R^2 = 0.91$ for both Greenland and U.K. soils (Fig. 5a)). The lag period had a maximum duration of around 20 h in both air-dried soil from Greenland and the U.K. No lag period was observed when soils were air-dried to about 14% WHC or higher before rewetting for both soils, suggesting a threshold where the response changes from a Type 2 into a Type 1 (Fig. 5a, vertical solid line).

The effect of moisture content before rewetting on the recovery

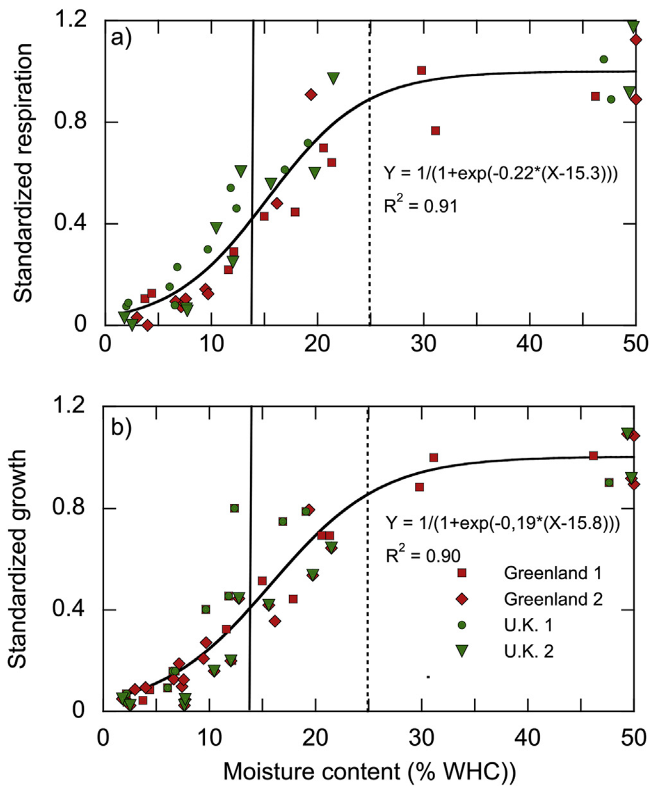

Fig. 2. Soil moisture content versus standardized respiration (a) and growth rates (b) before rewetting. Values were standardized by the maximum respiration and growth rates. Respiration and growth rate were fitted with a logistic equation. The vertical solid line indicates the transition from a Type 2 into a Type 1 response, and the vertical stippled line the transition between a Type 1 response and no effect of rewetting (see Fig. 5).

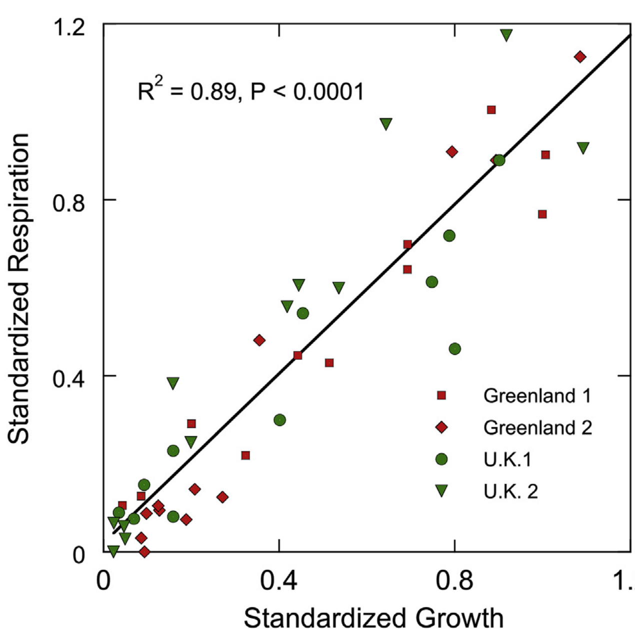

Fig. 3. The relationship between standardized bacterial growth and respiration at different moisture contents before rewetting the soil. Values were standardized by the maximum respiration and growth rates.

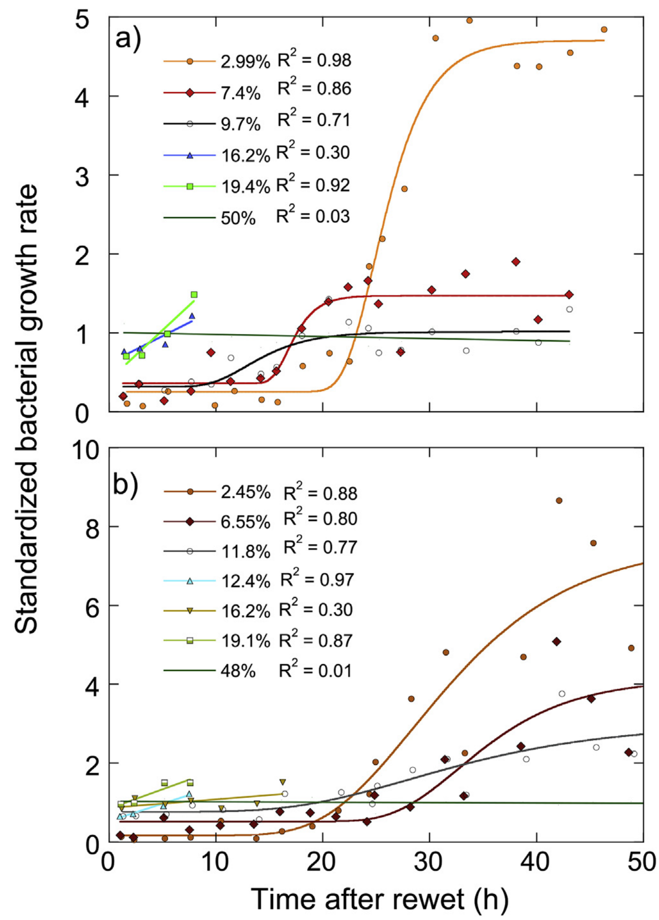

Fig. 4. Time after rewet versus standardized bacterial growth rate for soil from Greenland (a) and soil from U.K. (b). Values for the control soil with 50% WHC were set to 1. Six moisture contents were used for soil from Greenland and seven for soil from U.K. to illustrate when bacteria grew with a Type 1 pattern upon rewetting (diamond, circle), or a Type 2 pattern (triangle, square). The moist control is indicated with a green line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

time could be modeled with a logistic equation, with no differences between the soils (Table S1; $R^2 = 0.86$, Fig. 5b). The maximum time period for the bacterial growth to recover was around 23 h and occurred when soil was dried $\leq$5% WHC before rewetting. When soil was dried to around 25% WHC or higher, the modeled growth rate was not different from the moist control at 50% WHC, resulting in a recovery time of 0 h (Fig. 5b, vertical stippled line). Thus, above this threshold moisture content before rewetting there were no effect of rewetting the soil on the bacterial growth response.

The maximum bacterial growth rates found after rewetting were higher when soils were dried to a lower moisture content (i.e. more severe drying) before rewetting (Fig. 5c). For example, air-dried soil (3% WHC) had almost 5 times higher maximum growth rates after rewetting than the moist control for the Greenland soil, whereas soil with initial moisture content of 7.4% WHC had only ca. 1.5 times higher growth rates (Fig. 4a). The effect of partial drying on the maximum growth could be modeled with an exponential equation ($R^2 = 0.66$ for the U.K and 0.83 for Greenland soils, Fig. 5c). The maximum growth rate was around 5 times higher in air-dried soil than the constantly moist soils from Greenland and around 7 times higher in soils from the U.K. This maximum growth rate reached values matching those in the moist control at lower moisture contents for soil from Greenland compared to soils from the U.K. (Fig. 5c).

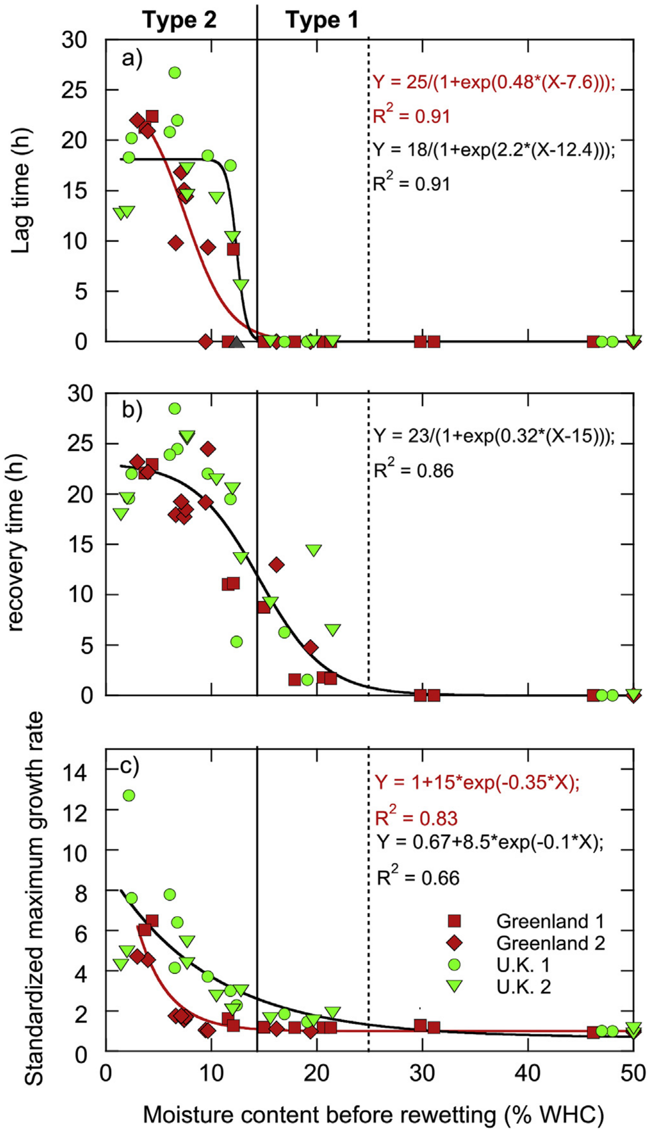

Fig. 5. Soil moisture content before rewetting versus bacterial growth characteristics: Lag time (a), recovery time (b) and standardized maximum growth rate after rewetting (c). Values for the control soil with 50% WHC were set to 1. Red lines and symbols indicate soil from Greenland (squares, diamonds) and green lines and symbols indicate soil from the U.K. (circles, triangles). Moisture content before rewetting and lag time was fitted with a logistic equation. The curve fit for recovery time was combined for both soils and could be fitted with a logistic equation. Standardized maximum growth rates were fitted with negative exponential equations. The vertical solid line indicates the transition from a Type 2 into a Type 1 response, and the vertical stippled line the transition between a Type 1 response and no effect of rewetting. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Respiration after rewetting

The drier the soil was before rewetting, the higher was the amount of respiration produced during 0–24 h (Fig. 6a) or during 24–48 h after rewetting (Fig. 6b). For air-dried soil, the respiration released during 0–24 h was 3 and 5 times higher than in the constantly moist soils from Greenland and U.K., respectively (Fig. 6a). The corresponding values for the time period 24–48 h were similar (Fig. 6b). Partial drying before rewetting decreased the amount of respiration released 0–24 h and 24–48 h after rewetting compared with air-dried soils ($R^2 \geq 0.81$ in all cases). An increased release of CO_2 after rewetting could only be detected when soil was dried below 12% WHC before rewetting for soil from Greenland and below around 20–30% WHC before rewetting for soil from the U.K. The respiration after rewetting from moisture contents above these values remained similar to the 50% WHC moist control soil during the entire experiment.

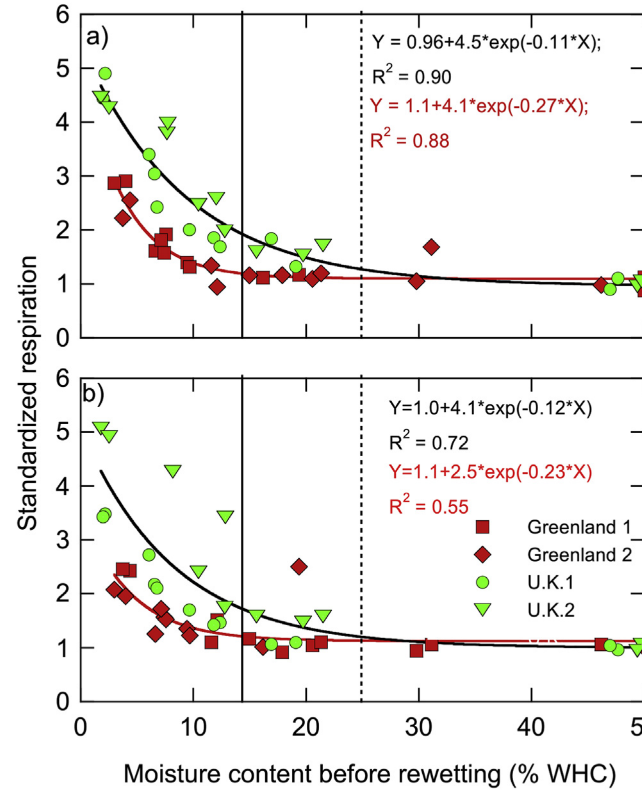

Fig. 6. Soil moisture content before rewetting versus standardized respiration rates during 0–24 h (a) and 24–48 h after rewetting (b). Values for the control soil with 50% WHC were set to 1. Curves were all fit with a negative exponential equation. The vertical solid line indicates the transition from a Type 2 into a Type 1 response, and the vertical stippled line the transition between a Type 1 response and no effect of rewetting (see Fig. 5).

4. Discussion

4.1. Partial drying is less severe than air-drying

We predicted that partial drying would be a less harsh treatment to the bacterial community compared to air-drying. Several lines of evidence support that the severity of drought increased with more complete drying, and could be reduced by incomplete, partial, drying. First, the level of bacterial growth immediately after rewetting has earlier been used as an index for the status of soil bacterial activity (Meisner et al., 2013, 2015), where higher growth rates show that bacteria have been less inhibited by drought and rewetting. The rate of growth directly after perturbation has also been similarly used to determine the status of the bacterial activity in soils following freezing-thawing (Koponen and Bååth, 2016). In the present study, bacterial growth was very low in air-dried soils, but the level increased with higher moisture in the partially dried soils (Fig. 2), thus suggesting that the latter treatments were less detrimental. Similar results have previously been observed for a Swedish grassland soil (Iovieno and Bååth, 2008) and for growth of cultivable bacteria (Seifert, 1961). Second, the respiration during the first 24 h after rewetting was highest in air-dried soils and decreased with more remaining water in partially dried soils (Fig. 6). This result is consistent with empirical and modeling studies of partial drying before rewetting (Fischer, 2009; Lado-Monserrat et al., 2014; Manzoni et al., 2016). Increased respiration rates due to harsher drying may capture substrate that became available from a more extensive killing of the microbial biomass induced by the drying and rewetting perturbation (Kieft et al., 1987; Fraser et al., 2016), by higher osmolyte concentration in microbial biomass induced by the drying (Warren, 2016), or by a higher C-release from SOM upon rewetting (Schimel et al., 2011). Still, lower respiration rates in partially dried soils suggested that partial drying before rewetting reduced the harshness of the perturbation. Increasing substrate release in more dried soils was also reflected by the maximum bacterial growth rate reached after rewetting, which was highest in air-dried soil and decreased with more remaining water in partially dried soils (Fig. 5c).

4.2. Reduced severity of drying changed the bacterial response from Type 2 to Type 1

We demonstrate that partial drying, with higher soil moisture remaining before rewetting, changed the response pattern of bacterial growth to rewetting from a Type 2 response (increase in growth after a lag period) into a Type 1 response (immediate increase in growth rates) (Figs. 1 and 4). As such, our results support our main hypothesis. It has previously been observed that a soil with a Type 1 response could be changed into a Type 2 response when air-dried for longer periods (Meisner et al., 2013, 2015), or when air-drying was combined with salt (Rath et al., 2017). The underlying reason for these changes were interpreted to be related to an increased harshness of drying to the bacterial community. We can now extend these results and also show that a milder and less severe drying event, partial drying, affects the bacterial growth response to rewetting in the opposite way, changing a Type 2 to a Type 1 response.

We also found evidence for a gradual transition in the extent of the Type 2 response in partially dried soils. The lag period grew shorter with higher moisture content before rewetting, to eventually reach zero, and thus transition into a Type 1 response (Fig. 5a). As predicted, this is the opposite effect of increasing the severity of drying, where extended periods of air-drying initially resulted in a transition from a Type 1 to a Type 2 response, with even longer lag periods after rewetting resulting from longer periods of air-drying (Meisner et al., 2015).

Our second objective was to determine at what moisture level a switch from a Type 2 to a Type 1 bacterial growth response would occur. This moisture threshold was around 14% WHC, in both soils (Fig. 5a). It is likely that soils with less pronounced Type 2 responses to drying-rewetting, *i.e.* with shorter lag-periods after rewetting from air-dried conditions, have threshold values for this transition at lower moisture contents.

There was also a gradual transition within the range of moisture contents in the partially dried soils that resulted in a Type 1 response after rewetting (>14% of WHC). The recovery time to levels of bacterial growth matching the moist reference soil became shorter with higher moisture content before rewetting up to ca. 24% WHC (Fig. 5b). Thus, for soils originally having a Type 1 response when rewetting air-dried soil (e.g. Iovieno and Bååth, 2008), partial drying is expected to still result in a Type 1 response but with shorter recovery times (also see section 4.5.).

4.3. Threshold moisture for no rewetting effect

A threshold moisture content of ca. 30% of WHC could be determined, above which drying and rewetting had no effect on growth (Fig. 5) or respiration (Fig. 6). Similar results have previously been reported for soil respiration upon partial drying, suggesting a moisture threshold for no effect (Fischer, 2009; Lado-Monserrat et al., 2014). The similarity of the threshold for cumulative respiration and maximum growth rate is consistent with increased substrate availability after rewetting driving both microbial variables. Furthermore, this suggests that respiration and bacterial growth are not affected by moisture changes within a relatively broad range centered around the expected optimal moisture (between ca. 30%–50% WHC in the studied soils).

4.4. The dependence of carbon-use efficiency on soil moisture and rewetting

The effects of environmental factors and perturbations on microbial carbon-use efficiency (CUE) have recently become an intense line of study, both empirically (Geyer et al., 2016; Öquist et al., 2016; Spohn et al., 2016a, 2016b) and theoretically (Wetterstedt and Ågren, 2011; Manzoni et al., 2012b; Roller and Schmidt, 2015). Although not explicitly studied here, comparing bacterial growth to respiration can provide an index for the microbial CUE as affected by moisture and rewetting events. CUE appeared to be stable under a wide range of stable moisture conditions, but low during the first 48 h after rewetting dry soils. Prior to rewetting when moisture levels were stable, respiration and bacterial growth were well correlated, with a near 1:1 relationship (Fig. 3), which is consistent with earlier laboratory experimental work (Iovieno and Bååth, 2008). This close correlation between growth and respiration suggests that different soil moisture levels will not affect CUE of soil bacteria during stable moisture conditions. However, after rewetting dry soil the link between growth and respiration was strongly uncoupled as initial growth rates were low and respiration rates were high. The underlying reasons for this disconnect have been previously discussed (Göransson et al., 2013; Meisner et al., 2013, 2015). Briefly, the initial respiration pulse is likely determined by substrate available for respiration without subsequent microbial growth. This interpretation is consistent with previous work on the source of the respiration pulse, which observed that both biochemical (extracellular) and organismal sources contribute to soil respiration when rewetting dry soil (Fraser et al., 2016). However, it remains to be resolved how the well-linked respiration and microbial growth during stable moisture balances against the dynamics triggered by variable moisture at ecosystem levels over longer time-periods.

4.5. Concluding remarks and outlook

We show that a soil with a Type 2 pattern in the bacterial growth response after drying-rewetting can be changed into a Type 1 pattern by partial rather than complete drying. We also suggest that the two response patterns of bacterial growth after rewetting dry soils are related to the amount of surviving microorganisms and thus to the harshness of drying.

Adding these observations to results from earlier studies, we propose a generalized conceptual figure to describe how the bacterial response to rewetting dry soil is determined by the harshness of drying (Fig. 7). Increasing harshness has been shown to occur with increasing duration of drought, or drought combined with altered osmotic conditions due to salt, and decreasing harshness due to partial drying. In addition, different soils can respond to rewetting from different positions along the 'harshness scale' when they are air-dried for 4 days (see A, B and C in Fig. 7 and description in legend). We choose soils in the present study at the high end of the harshness scale with a Type 2 response and long lag periods (A in Fig. 7). Soils with a Type 2 response, but with only a short lag

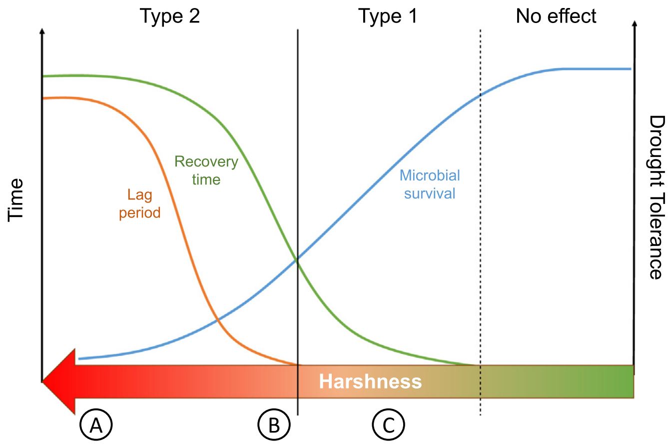

Fig. 7. A schematic overview of the response patterns of bacterial growth to drying-rewetting and their dependence on the harshness of drying. An increasing harshness of the drying event is depicted on the x-axis with increasingly detrimental perturbations for the microbial community oriented to the left-hand side. Increasing harshness can be achieved by extended duration of drought (Meisner et al., 2013, 2015) or drying to lower moisture content before rewetting (present study). For the latter case, starting to the right, at optimal moisture conditions, going left along the x-axis, at a threshold value of moisture (vertical stippled line), bacterial growth will be impaired, but will rapidly recovery after rewetting, resulting in Type 1 response. A longer recovery time is found in harsher treatments (further to the left). The transition from a Type 1 to a Type 2 response (solid vertical line) is indicated by the presence of a lag period before exponential growth. This lag period will be short near this threshold, but lag period and recovery period will increase with harsher treatments (e.g., more extensive drying or longer periods of drought). Soils from different locations that are air-dried for 4 days can have different response patterns after rewetting. Soils studied here are at the high-end of the "harshness scale" (A), soils having a Type 2 response but with only a short lag period further to the right (B), and soils with a Type 1 response even further to the right (C).

period after 4 days drying (B in Fig. 7), are predicted to change to a Type 1 response when partially dried to a moisture content only marginally wetter than air-dried conditions before rewetting. Prolonged droughts, on the other hand, will always result in Type 2 responses for these soils for all points on the harshness scale, but with longer lag periods correlating to length of drought. Soils with initially a Type 1 response after air-drying-rewetting (C in Fig. 7), would be predicted to only decrease the recovery time with partial drying, whereas prolonged droughts would result in a transition to a Type 2 response with longer lag periods with increasingly longer drought periods (Meisner et al., 2015).

One question that remains unanswered is how identical experimental drying-rewetting treatments (air-drying during 4 days) can result in two response patterns in different soils? Different physio-chemical environmental factors affecting microbial survival and respiration may be one reason (Balogh et al., 2011; Kaiser et al., 2015). Another explanation may be that microorganisms from different climates are adapted to different moisture regimes with differences in microbial drought tolerance affecting the response pattern (Allison and Goulden, 2017). In order to identify the mechanisms underpinning different response patterns, we thus need to study the microbial responses to drying-rewetting in soils from different regions, including wide ranges of edaphic factors and with different legacies of drought and rewetting episodes.

An additional aspect to consider is the moisture content the soil is rewetted to after drying (Rey et al., 2017). This was not studied here, since soils were always rewetted to 50% WHC. However, moisture levels post-rewetting may be important for the bacterial response, since more CO_2 is produced when dry soil is rewetted to higher water content after rewetting (Evans et al., 2014; Lado-Monserrat et al., 2014). We expect, however, that the response type of bacterial growth would be mainly determined by amount of remaining water prior to rewetting due to the importance of the harshness of drying in determining the growth pattern after rewetting shown here.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.05.016.

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